

## MARINE BIOLOGY

# Dinoflagellate Cysts in the Surface Sediments of the White Sea

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**Abstract**—Dinoflagellate cysts were studied in 42 samples from the surface sediments of the White Sea. The total concentration of dinocysts varies from single cysts to 25000 cyst/g of dry sediments, which reflects the biological productivity in the White Sea waters and the regional particular features of the sedimentation processes. The highest concentrations are observed in silts; they are related to the regions of propagation of the highly productive Barents Sea waters in the White Sea. Generally, the spatial distribution of dinocysts species in the surface sediments corresponds to the distribution of the major types of water masses in the White Sea. The cysts of the relatively warm-water species (*Operculodinium centrocarpum*, *Spiniferites* sp.) of North Atlantic origin that dominate in the sediments indicate an intensive intrusion of the Barents Sea water masses to the White Sea along with hydrological dwelling conditions in the White Sea favorable for the development of these species during their vegetation period. The cold-water dinocyst assemblage (*Islandinium minutum*, *Polykrikos* sp.) is rather strictly confined to the inner parts of shallow-water bays, firstly, those adjacent to the Onega and Severnaya Dvina river mouths.

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## INTRODUCTION

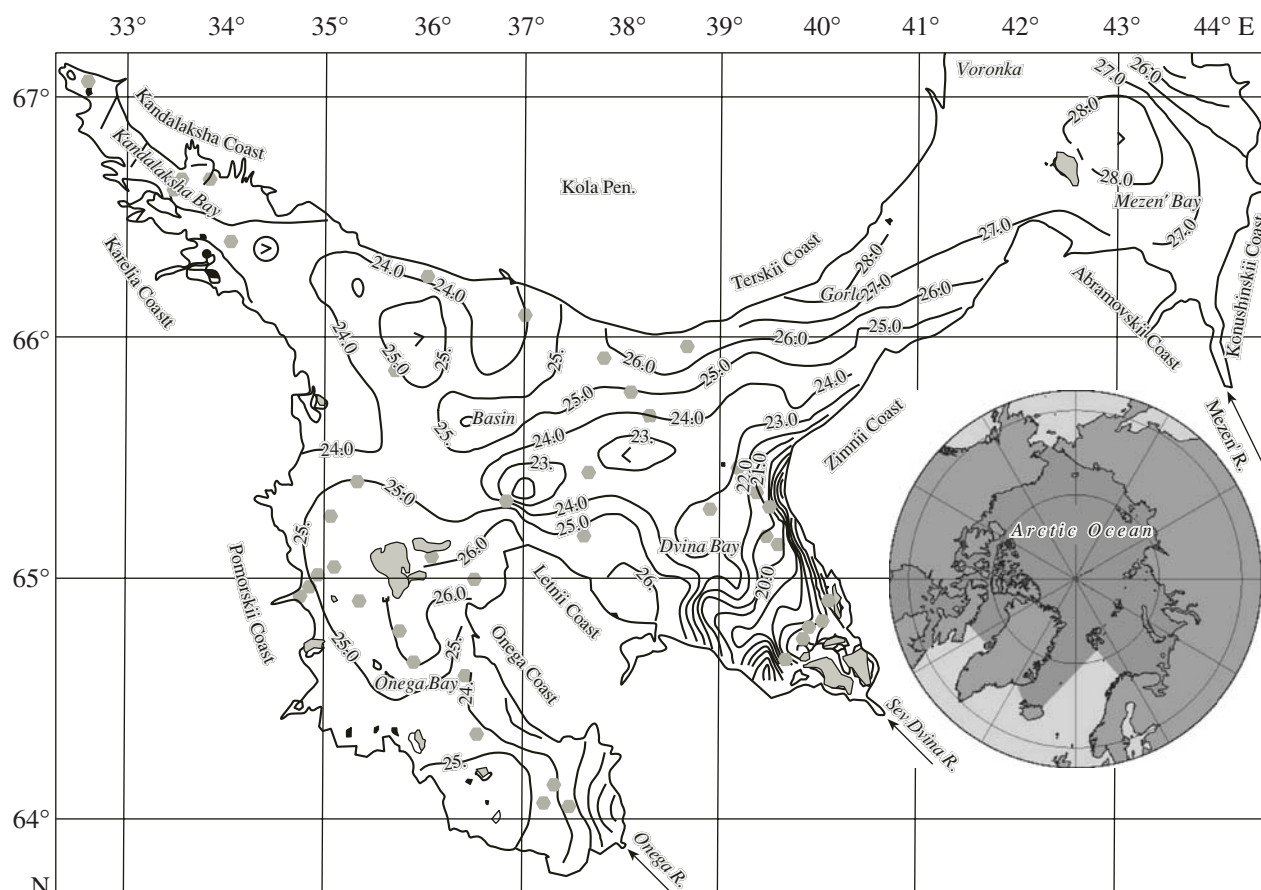
Up to recently, the micropaleontological groups that have been leading in the stratigraphic and paleoceanological studies of the Arctic seas were almost exclusively diatoms; foraminifers; spores and pollen; and, partly, ostracodes. During the past years, the microfossil group included, first of all, dinoflagellate cysts, green algae, acritarchs, and organic portions of foraminifer skeletons and other organic remains of aquatic microorganisms [28, 34, 36]. Among the aquatic objects, the most informative for paleoceanological reconstructions are cysts of dinoflagellates (dinocysts), which allow one to reconstruct various parameters of the water masses such as the temperature and salinity of the surface seawaters, the presence of sea ice, and the origin and distribution of the main types of water masses [27, 35]. Freshwater green algae, along with their quantitative relation to dinoflagellate cysts, may be used as indicators of the riverine runoff and changes in its intensity [34].

Dinoflagellates—unicellular microorganisms with a wide food spectrum—are, together with diatoms, one of the principal components of the phytoplankton of the shelf Arctic seas [18]. Meanwhile, only one-fifth of them form cysts that can be conserved in the sediments [30, 34]. In the recent years, the studies of the dinocysts of the Arctic seas have made great progress and allowed scientists to reveal the general regularities of their composition and distribution in the bottom sediments depending on the hydrological and ice conditions of the

shelf [26, 30, 31, 35, 40, 46]. Up to the present, for this group of microfossils with different degrees of detailing, the characteristics of the species and quantitative compositions of their assemblages in the sediments of almost all of the Arctic seas have been obtained except for in the East Siberian and White seas. Thus, the results of dinocyst studies in the surface sediments of the White Sea presented in this paper represent the first information on the group considered, which allows one to use it in the paleoenvironmental reconstructions of the White Sea.

## MATERIALS AND METHODS

This report is based on the materials collected during cruise 49 of R/V *Professor Shtokman* on August 2–22, 2001; the cruise of R/V *Ekolog* in September 2002; and in the expedition of R/V *Ivan Petrov* in July 2002 in the White Sea. The collection and lithological description of the samples were performed by the scientists of the Laboratory of Physical–Geological Studies of the Shirshov Institute of Oceanology of the Russian Academy of Sciences. A total of 42 samples of the surface (0–5 cm) sediments were selected for the analyses (Fig. 1, Table 1); the preliminary results of their processing were partly published [39]. The samples were collected with the use of an Okean-0.25 grab sampler and placed in plastic bags. After vacuum drying executed at the Schmidt Russian–German Laboratory of the Arctic and Antarctic Research Institute (AANII) in St. Petersburg, subsequent processing was performed



**Fig. 1.** Distribution of the mean interannual summertime salinity of the surface waters of the White Sea [1]. The dots represent the location of the samples of the surface sediments studied (see Table 1 for coordinates).

following the technique applied for the program bottom sediment samples at the Alfred Wegener Institute for Polar and Marine Research (AWI) in Potsdam. According to this technique, in order to dissolve carbonates and silicon-containing particles, HCl and HF were used [23, 38]. To remove particles smaller than 10  $\mu\text{m}$  from the sample, the preparations were filtered using filters 47 mm in diameter with a pore size of 7–10  $\mu\text{m}$ . The filtered sediment, which contained dinoflagellate cysts, was added to glycerin. The examination of the microfossils was performed with the help of a Neovar 2 light microscope at a magnification of  $\times 400$ . In each of the samples, at least 100 dinoflagellate cysts were identified. The addition of tablets with spores of *Lycopodium clavatum* to the preparations allowed us to count the cyst concentration in the sediment (number of cysts per gram of dry sediment) using the method described by Stockmarr [45].

#### PRESENT-DAY ICE AND HYDROLOGICAL CONDITIONS OF THE WHITE SEA

The White Sea is almost entirely located south of the Polar Circle. It belongs to the basin of the Arctic Ocean

and is the most isolated sea from it (Fig. 1). It is connected with the Barents Sea via a shallow-water strait and has an area of 91 th. km<sup>2</sup> [2, 10]. This minor sea basin is characterized by significant sea depth increments [2, 21, 24]. The average sea depth equals about 67 m; the maximal depths are registered in the central depression (the Basin of the White Sea) and in Kandalaksha Bay, where they reach 350 m. With respect to the structure and geomorphology, one can distinguish the Voronka, the Gorlo, the Basin, and four major bays: Onega, Dvina, Mezen', and Kandalaksha bays. They differ in the regimes of the freshwater supply, influence of tides, salinity gradients, ice conditions, and biota [2, 13, 29].

Presently, within the framework of modern concepts, the White Sea is regarded to represent a hierarchic estuarine system. The upper level of the hierarchy is the entire sea, within which two water masses occur (the White Sea mass with a salinity of 25–30‰ and the Barents Sea mass with a salinity of 34–35‰). When changing the scale of the consideration, the sea becomes a system of four bays–estuaries rather than a single estuary [37].

**Table 1.** Geographical location of the samples studied in the White Sea. The lithological composition of the surface sediments and the concentrations of dinoflagellate cysts are converted to 1 g of dry sediment

Sample nos.	Coordinates		Lithological composition of the sediments	Dinocyst concentration (cyst/g of dry sediment)
	Latitude, N	Longitude, E		
Cruise 49 of R/V <i>Professor Shtokman</i> , August 2001				
PSh-4684	64°45.65′	39°42.40′	Well washed fine-grained sand	<100
PSh-4687	64°40.66′	39°32.98′	Fine-grained sand	<100
PSh-4693	64°48.53′	39°46.17′	Silty fine-grained sand	<100
PSh-4694	64°48.38′	39°54.82′	Sandy silt	4200
PSh-4697	65°17.03′	38°54.90′	Sandy–clayey silt	3000
PSh-4699	65°40.80′	38°16.29′	Silty–clayey ooze	2200
PSh-4700	65°46.97′	38°03.09′	Liquid silty–clayey warp	5500
PSh-4701	65°55.31′	37°50.87′	Liquid silty–clayey warp	5200
PSh-4702	65°26.09′	37°41.98′	Liquid silty–clayey warp	5900
PSh-4703	65°11.09′	37°35.39′	Liquid silty–clayey warp with an admixture of sand grains	2500
PSh-4704	65°19.07′	37°35.39′	Liquid silty–clayey warp	10 500
PSh-4705	65°01.20′	36°34.03′	Silty–clayey warp	<100
PSh-4706	65°05.24′	36°05.47′	Unsorted silty sand, sometimes gravel	4700
PSh-4709	64°35.29′	36°26.94′	Pebbles and gravel in the matrix of liquid clayey varigrained sand	750
PSh-4712	64°08.90′	37°19.66′	Weakly clayey sand with coquina and pebbles	300
PSh-4713	64°21.91′	36°32.41′	Unsorted sediment from sand, gravel, and pebbles	<100
PSh-4714	64°39.30′	35°52.65′	Clayey silty sand	3000
PSh-4716	65°16.24′	35°04.83′	Clayey fine-grained sand	9500
PSh-4717	65°24.19′	35°21.13′	Sandy–clayey silt	5900
PSh-4719	65°51.31′	35°43.16′	Liquid silty clay	4400
PSh-4720	65°57.26′	35°53.52′	Silty–sandy clayey warp	<100
PSh-4721	66°39.35′	33°38.56′	Strongly clayey medium- and fine-grained sand	2700
PSh-4722	66°35.91′	33°29.30′	Sandy–clayey silt	5100
PSh-4724	66°09.56′	35°02.18′	Silty–clayey warp	5700
PSh-4728	65°21.00′	39°21.30′	Sandy–clayey warp	3200
R/V <i>Ekolog</i> , September 2002				
3	66°19.80′	33°39.84′	Silt	10 500
4	67°08.10′	32°23.20′	Silt	7200
10	65°00.53′	34°49.84′	Silty clay with an admixture of coarse-grained sand	<100
15	66°39.95′	33°50.23′	Silt	4600
16	64°58.65′	34°47.84′	Silty clay	<100
32	64°06.93′	37°35.07′	Weakly clayey sand with coquina and pebbles	2500
40	65°02.05′	34°53.79′	Silty clay with an admixture of poorly rounded pebbles	<100
43	64°11.42′	37°36.65′	Weakly clayey sand with coquina and pebbles	<100
59	66°20.04′	35°32.02′	Silt	22 000
62	64°49.19′	35°43.33′	Silt	3600
75	65°26.89′	39°04.18′	Silt	19 900
76	65°17.00′	39°16.62′	Silt	12 000
77	65°08.69′	39°16.95′	Silt	3000
78	65°05.08′	39°44.15′	Silt	<100
88	64°55.49′	40°01.82′	Fine-grained sand	3900
Cruise 52 of R/V <i>Ivan Petrov</i> , the end of June to the beginning of July 2002				
IvP 39	66°34.70′	33°47.10′	Silt	17 100
IvP 40	66°25.70′	33°56.10′	Silt	13 900

The present-day hydrological region of the White Sea is mostly formed under the influence of the desalinating riverine runoff and the water exchange with the Barents Sea. To a significant extent, the abundant riverine runoff (~225 km<sup>3</sup>/year) [4] defines the regularities and particular features of the biochemical processes within its area. The particularity of the continental runoff lies, first of all, in the fact that all the rivers fall into the Dvina, Onega, and Mezen' bay, i.e., isolated sea areas, which determines the strongly irregular distribution of the salinity of the surface seawaters (Fig. 1). In so doing, the maximal runoff values, as well as those of the supply of particulate matter and nutrients, are observed in the springtime full warm-water period in May [4, 14].

The particulate matter is one of the principal forms of the matter transfer [13], and its elevated or reduced content in the water directly influence the ecological balance in the aquatic area. Phytoplankton, being a constituent of the particulate matter, is part of a long food chain, and its mineral particles (at their high contents) attenuate the solar flux to the deeper layers and retard the development of living organisms [13].

The water exchange with the Barents Sea is implemented via a narrow shallow-water strait—the Gorlo of the White Sea (Fig. 1). The permanent gravity current of the desalinated surface waters to the Barents Sea (with a discharge of ~2200 km<sup>3</sup>/year) runs along the Zimnii Coast of the White Sea. A reverse flow of heavy normally saline oceanic waters (~2000 km<sup>3</sup>/year) is directed from the Barents Sea via the Gorlo; this way, approximately two-thirds of the deep White Sea water is annually renewed [4, 17, 24].

The most important features of the hydrological regime of the White Sea is represented by tides; they reach their maximal heights (up to 10 m) in Mezen' Bay. The intensive tidal movements provide strong vertical mixing of the waters; therefore, in the regions with relatively small sea depths (for example, the Gorlo and Onega and Mezen' bays), there is virtually no vertical stratification [2, 21, 24].

The summertime temperatures of the surface waters in the White Sea range from +7 to +15°C; in the winter-time, the temperatures fall down to –1.6°C in the north and to –1.7°C in the south. The riverine waters, which desalinate mainly the southeastern part of the sea (Fig. 1), provide additional conditions for the formation of the ice cover. From November to May, the sea is covered with drifting ice; in the bights near river mouths, fast ice is formed. Due to this reason, the White Sea is characterized by ice conditions that are more severe than those characteristic of the corresponding latitudes; this affects the dynamics of the biological productivity of phytocoenoses [8, 41, 42]. In addition to the local impacts, due to the exchange currents between the Barents and White seas, the sea ice that was formed

in the inner basin is supplied to the Arctic Ocean, where it takes part in the global thermohaline cycling [22].

The spatial inhomogeneities in the halocline parameters are determined by the horizontal advection, the contacts between water masses of different origins, the riverine runoff distribution, and the intensity of the biochemical processes [6, 15]. The horizontal circulation is the principal mechanism of the redistribution of elements over the sea area. According to different estimates, the mean annual productivity of phytoplankton of the White Sea varies from 13 to 95 g C/m<sup>2</sup> [3, 5–7, 11, 15, 16, 24] and features two seasonal peaks related to the spring and summer. In so doing, the peak of the dinoflagellate development follows the summertime peak of the development of diatomaceous algae.

## DINOCYSTS IN THE SURFACE SEDIMENT LAYER OF THE WHITE SEA

Dinoflagellates represent one of the leading groups of phytoplankton and the principal biological producers of the White Sea [6, 8, 19, 20, 41, 42]. A revision of the systematic composition of the White Sea dinoflagellates [19, 42] showed that, with respect to the species number, the phytoplankton of the White Sea is rich as that of the Barents Sea [6]. Meanwhile, the reduced salinity of the White Sea waters hampers the development of selected stenohaline species typical of the Barents Sea, while the high seasonal temperature gradients result in the absence of a series of cold-water Arctoboreal species. The flora of the White Sea contains no less than 50% of the Barents Sea species. According to the phytogeographical characteristics of the species [44], the planktonic flora of the White Sea belongs to the Arctoboreal domain; meanwhile, the proportion of Arctoboreal species (15%) in the dinoflagellate composition is lower as compared to diatoms. The group of dinoflagellates, in contrast to the other phytoplankton components, features the highest proportion of boreal species (13%). Along with this, the intensive water exchange with the Barents Sea provides a high species diversity of the Arctoboreal–tropical (14% in the composition of dinophyta algae) and cosmopolitan (up to 28%) species, which are never or rarely encountered in the Siberian seas of Eurasia [18].

### *Quantitative Distribution of Dinocysts in the Sediments*

The sediments of the White Sea studied are distinguished by a relatively high diversity of the grain-size composition: from fine-grained sands to silty clays (Table 1). The sizes of dinoflagellate cysts range from 32 to 100 µm, which corresponds to the coarse-grained silt fraction of the White Sea sediments. The maximal dinocyst concentrations (up to 22000 cyst/g of dry sediment) were registered in the silty fractions of the surface sediments (Fig. 2), which confirms the regularities



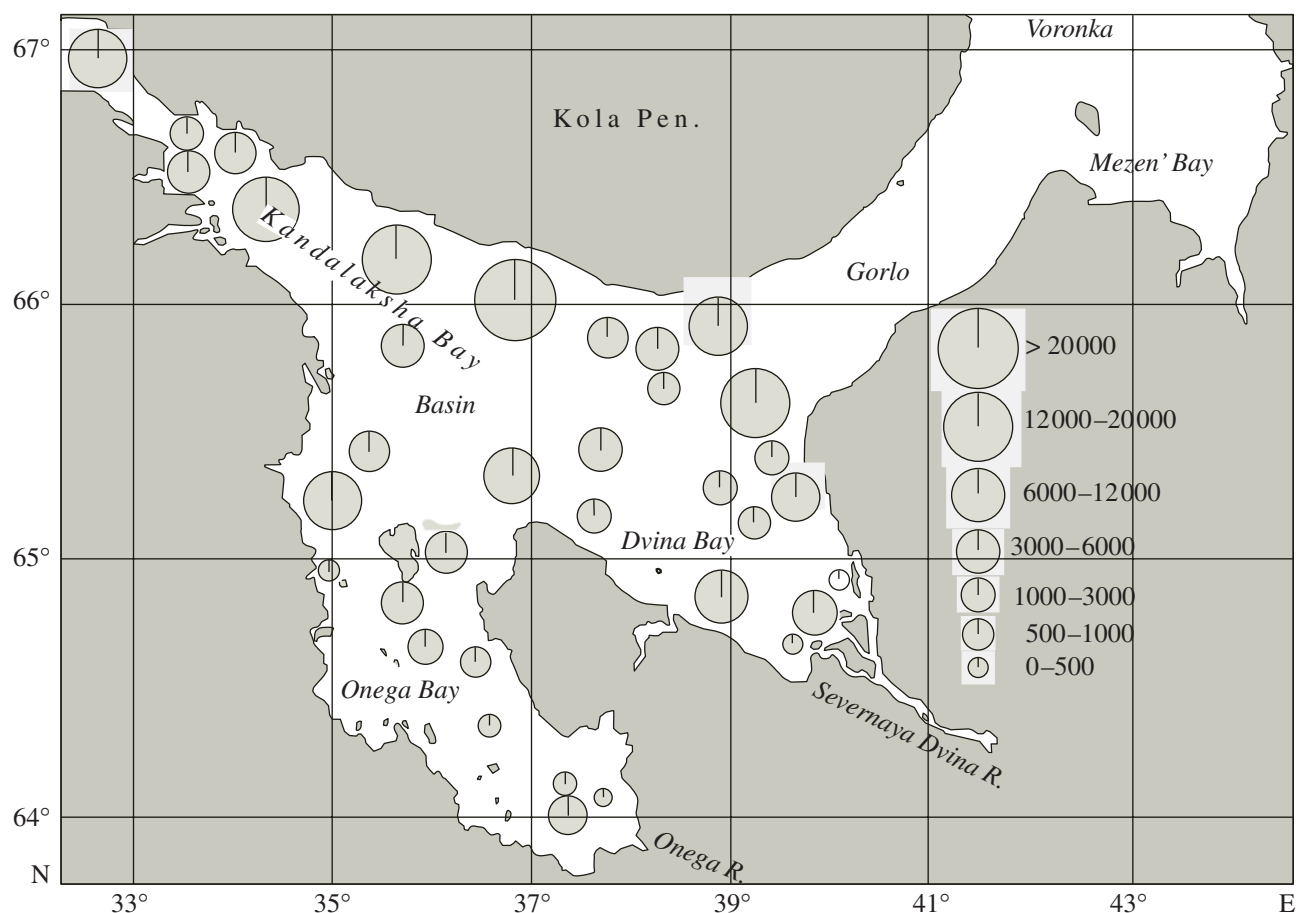


Fig. 2. Concentrations of dinoflagellate cysts in the surface sediments of the White Sea, cyst/g of dry sediment.

of the cyst distribution in the sediments revealed earlier [25]. The minimal concentrations ( $<100$  cyst/g of dry sediment) were encountered in the fine-grained sands, which are usually perfectly washed. In the sands with various admixtures of silty and clayey matter, the concentrations of dinoflagellate cysts comprise from a few tens to 9500 cyst/g of dry sediment. From this fact, one can conclude that the enhanced dinocyst concentrations in the Central Basin and their reduced values in bays may be related to the grain-size composition of the White Sea sediments. Another factor that restricts the dinocyst contents in the sediments is the salinity of the surface seawater. Dinoflagellate cysts, as derivatives of marine phytoplankton, were encountered in the samples from the White Sea within the salinity interval from 15 to 25‰.

#### *Dinocyst Species in the Surface Sediments*

Thirteen dinocyst species were identified in the surface sediments of the White Sea (Table 2); this comprises approximately one-eighth of the dinoflagellate species ever registered in the plankton of this sea [6, 42].

The dominating species *Operculodinium centrocarpum* (Fig. 3) is a widely spread cosmopolitan species; this is confirmed by the ecology of this cell during its mobile stage (biological taxon *Protoceratium reticulatum*). This dinoflagellate species is a neritic species widely spread in seas and oceans of the boreal zone [30, 32, 34]. Another dominating cyst species *Pentaparthodinium dalei* (*Scrippsiella trochoidea*), in contrast to those previously mentioned, refers to the *Peridinium* group and is also a cosmopolite that is mostly distributed in the Northern Hemisphere [9]. Cysts of these species dominate (up to 76%) in the northern and central regions of the White Sea. The species *Spiniferites ramosus* (Table 2) is also cosmopolitan and is most abundant in the zones of mixing of the surface waters [32, 43]. In the White Sea, this species is most spread (up to 51%) in the unstratified waters of Onega Bay. The heterotrophic marine species typical of polar and subpolar regions of the Arctic shelf seas such as *Islandinium minutum* and similar morphotypes (*I. cesare* and *Echinidinium karaense*) are widely spread in wide temperature and salinity ranges; they are capable of dwelling over 8–12 months under the conditions of sea ice cover [9, 27, 32] and are most abundant (up to 33%)

**Table 2.** Species composition of dinoflagellate cysts in the White Sea

Dinoflagellates cysts	Biological denomination	Ass. 1	Ass. 2
<i>Bitectatodinium tepikiense</i> Wilson	<i>Gonualax digitalis</i> (Pouchet) Kofoid	+	
<i>Brigantedinium cariacense</i> (Wall). Reid	<i>Protoperidinium cf. avellanum</i> (Meunier) Balech		+
<i>Brigantedinium simplex</i> (Wall). Reid	<i>Protoperidinium conicoides</i> (Paulsen) Balech		+
<i>Echinidinium karaense</i> Head, Harland & Matthiessen	Protoperidiniaceae		+
<i>Islandinium minutum</i> Harland & Reid	Protoperidiniaceae		+
<i>Islandinium? cezare</i> de Vernal et al	Protoperidiniaceae		+
<i>Operculodinium centrocarpum</i> Wall & Dale 1966	<i>Protoceratium reticulatum</i> (Claparende & Lachmann) Diesing	+	
Cyst of <i>Pentapharsodinium dalei</i> Indelicato & Loeblich	<i>Scrippsiella trochoidea</i> (Stein) Balech	+	
Cyst of <i>Polykrikos</i> sp. Arctic morphotype Kunz-Pirrung	<i>Polykrikos</i> sp. Kunz-Pirrung		
<i>Selenopemphix quanta</i> (Bradford) Matsuoka	<i>Protoperidinium conicum</i> (Gran) Balech		+
<i>Spiniferites elongatus</i> Reid	<i>Gonualax elongata</i> (Reid) Ellegaard	+	
<i>Spiniferites ramosus</i> Mantell	<i>Gonualax spinifera</i> (Claparende & Lachmann) Diesing	+	
<i>Nematosphaeropsis labyrinthus</i> (Ostenfeld) Reid	<i>Gonualax spinifera</i> (Claparende & Lachmann) Diesing	+	

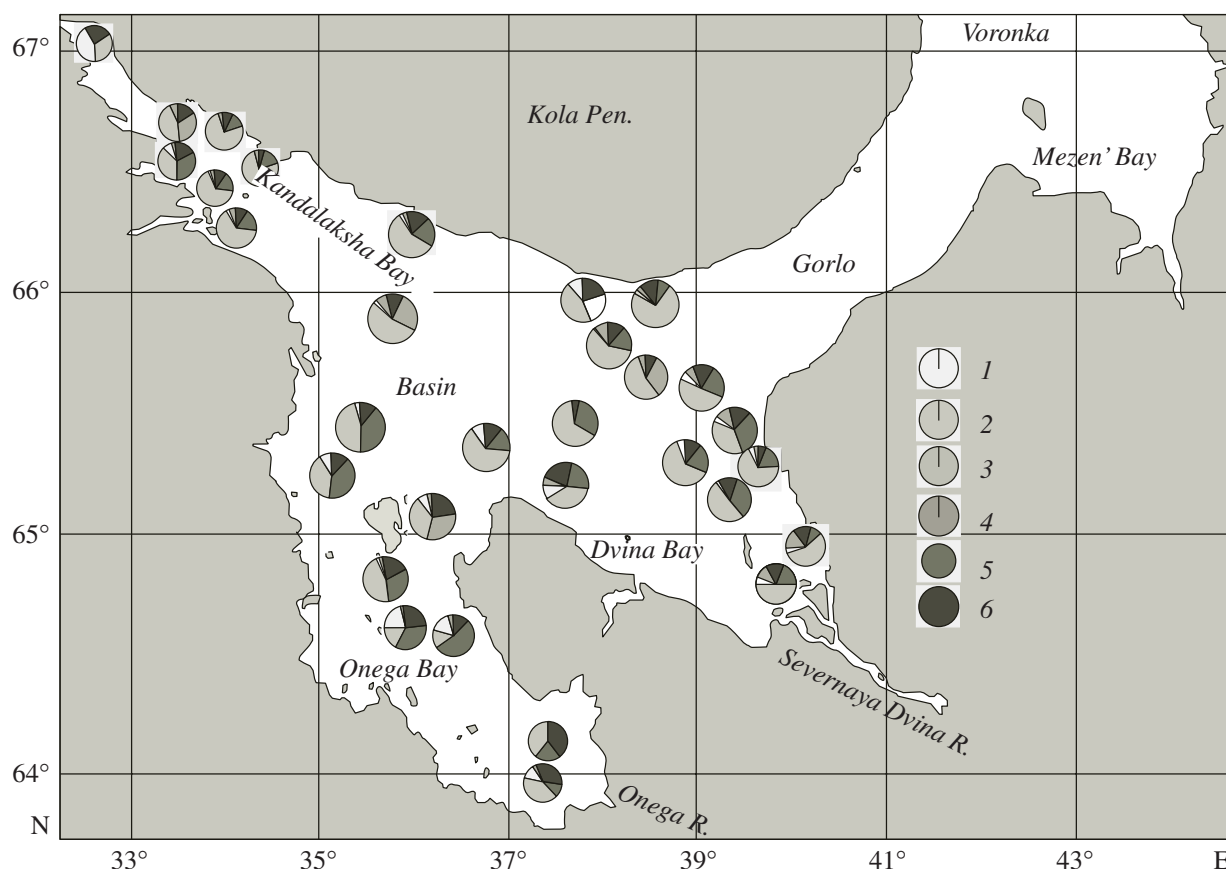
Note: Dinoflagellate associations: Ass. 1—autotrophic species; Ass. 2—heterotrophic species.

in the central and southern parts of the White Sea. The cysts of the neritic species *Brigantedinium cariacense* and *Brigantedinium simplex* (Table 2, [35, 36]) widely spread in cold waters are characteristic of the northern and central regions of the sea, where their integrated abundance reaches 42%. They refer to heterotrophic planktonic dinoflagellate species of the genus *Protoperidinium*. The species *Selenopemphix quanta*, which is highly tolerant to the salinity and temperature of the surface waters, features its highest abundances (up to 18%) in Dvina Bay. In plankton, cells of this species are widely spread in cold, temperate, and warm waters [9].

Other dinocyst species are not abundant in the White Sea; their total content never exceeds 10%. Meanwhile, their ecological and phytogeographical characteristics may provide additional information on the hydrological environments. Cysts of *Polykrikos* sp. Arctic morphotype, first identified in 2001 [31], are characteristic (up to 2%) of Kandalaksha and Dvina bays. Cysts of *Bitectatodinium tepikiense*, which also refers to widely spread tropical–boreal notal species [9], are encountered in the northern part of the Basin and in Dvina Bay (up to 5–10%). Species of the *Nematosphaeropsis* genus are cosmopolites and, at their planktonic stage, refer to the *Gonualax spinifera* species as well as species of the *Spiniferites* genus. In the sediments of the White Sea, they feature small abundances (up to 1%) and are mostly encountered in the central parts of the sea.

#### Regional Features of the Formation of Dinocyst Associations in the Surface Sediments

**Onega Bay** is one of the most shallow-water bays of the sea. Its waters are formed under the influence of an intensive riverine runoff and of the waters of the Basin that penetrate into the most deep-water northern part of the bay via the Zapadnaya Solovetskaya Salma Strait [47]. The waters of the northern part are characterized by a higher salinity (25–26‰) and a lower temperature [47]. Onega Bay is an estuary with the most complicated mosaic structure of the bottom topography, islands, and water stratification [37]. In this region, the composition of the dinocysts in the surface sediments is absolutely dominated by the autotrophic cosmopolitan species *Operculodinium centrocarpum*, *Pentapharsodinium dalei*, and *Spiniferites* spp. (up to 50%) at high contents of heterotrophic species such as *Islandinium minutum* and *Polykrikos* sp. Arctic morphotype (Fig. 3). The maximal concentrations of *Operculodinium centrocarpum* and *Pentapharsodinium dalei* reach 1700 cyst/g of dry sediment at their relative proportion in the associations up to 37%. The concentration of *Spiniferites* species (40–50% of the associations) changes from 380 to 1400 cyst/g while moving toward the Solovetskie Islands. The prevalence of autotrophic species in the dinocyst associations of the surface sediments of Onega Bay is probably related to the composition of the phytoplankton and the temperature conditions favorable for the development of dinoflagellates during the vegetation period. Along with this, the elevated percentages of the heterotrophic species *Islandinium minutum* and



**Fig. 3.** Percentages of species and species groups of dinoflagellate cysts in the surface sediments of the White Sea, % of the total dinocyst abundance in the samples: 1 – *Brigantedinium* sp. Wall 1965; 2 – *Operculodinium centrocarpum* sensu Wall & Dale 1966; 3 – *Selenopemphix quanta* (Bradford 1975) Matsuoka 1985; 4 – *Spiniferites elongatus* Reid 1974; – *Spiniferites* spp. Mantell 1850; 5 – *Islandinium cezare* de Vernal 1989; – *Islandinium minutum* Harland & Reid 1980; 6—others.

close morphotypes (*I. cezare*, *Echinidinium caraense*) are probably caused by the elevated concentrations of particulate matter in the unstratified waters of the bay (up to 13–14 mg/l) at the river–sea barrier during the period of the maximal development of planktonic dinoflagellates [13].

**Kandalaksha Bay** is the most deep-water bay characterized by a relatively quiet hydrological regime and a stable water stratification in the summertime period [6, 37]. This wide and deep estuary features the most irregular coastline and inhomogeneous riverine runoff in different parts of the bay. In its water structure, three water masses are distinguished, namely, the surface, intermediate, and near-bottom water masses [6, 37]. At the particulate matter concentrations from less than 0.2 mg/l in the central part of the bay to 1 mg/l in its top part [13], the dinocyst contents in the sediments of the central part of the bay reach 17100 cyst/g and increase to 22000 cyst/g toward the central depression (Fig. 2). The reason for the high concentration values in the deep-water areas of Kandalaksha Bay probably lies in the domination of silty sediments, in contrast to the shallow-water regions, where sandy fractions prevail

[47]. Autotrophic species such as *Operculodinium centrocarpum* and others dominate (up to 76%) in the composition of the dinocyst associations in the surface sediments (Fig. 3), and their total concentrations in the sediments of the top part of the bay and in its middle most open part comprise 3000 and 13000 cyst/g, respectively. Along with the autotrophic species, heterotrophic species such as *Islandinium minutum* and its close morphotypes are present (up to 18% of the dinocyst composition at the total concentration up to 2500 cyst/g of dry sediment). Cysts of the tropical–boreal species *Polykrikos* sp. *Arctic morphotype* comprises 1–2%. On the whole, the cysts of heterotrophic species are mainly confined to the shallow-water regions of the bay, in contrast to the cysts of autotrophic species, which are spread in the open parts of the sea characterized by a higher transparency (Fig. 3). This is also confirmed (Table 2) by the presence of the *Spiniferites* species (with a total content up to 32% in the dinocyst composition) confined to the areas with the minimal particulate matter contents near the Solovetskie Islands; this agrees with both satellite and expeditionary data [13]. Of heterotrophic species, *Sele-*

*nopemphix quanta* (up to 10%) is encountered in the top part of Kandalaksha Bay.

**The Basin of the White Sea** occupies the central part of the sea with sea depths of 100–300 m. The surface sediments of the Basin are characterized by constantly high dinocyst concentrations (more than 7000 cyst/g of dry sediment) (Fig. 2). The autotrophic species *Operculodinium centrocarpum*, *Pentapharsodinium dalei*, and others (up to 65% in the composition of the associations) and species of the *Spiniferites* genus (up to 40%) dominate marking the zones with the lowest particulate matter contents (Fig. 3). In the central part of the Basin, *Nematosphaeropsis* sp. was noted; with respect to the feeding type, it is an analog of *Operculodinium centrocarpum*, although it dwells at greater depths [30, 32, 34]. **Dvina Bay** is located in the eastern part of the White Sea and represents a wide stratified estuary with the maximal runoff of the Severnaya Dvina River. Here, the particulate matter content is characterized by an increase in its concentration toward the Zimnii Coast, along which the major part of the riverine runoff is transported with concentrations from 1 to 5.56 mg/l in the autumn period [13]. With the distance from the river mouth toward the Basin of the White Sea, the dinocyst concentrations grow from 400 to 5000 cyst/g, which generally corresponds to the changes in the grain-size composition of the sediments (Fig. 2). The maximal concentrations (up to 20000 cyst/g of dry sediment) were registered at the exit from the bay toward the Gorlo, where active water exchange with the Barents Sea occurs. Here, the dinocyst composition is dominated by the autotrophic species *Operculodinium centrocarpum*. In the top part of the bay, in the region of the operation of the marginal filter [12], an enhanced concentration (up to 40%) of dinocysts of the heterotrophic species *Islandinium minutum* and *Impagidinium pallidum*, whose presence was related to the high water turbidity, and a decrease in the number of autotrophic species were noted.

#### *Principal Types of Dinocyst Associations in the Surface Sediments of the White Sea*

An analysis of the species composition of the dinoflagellate cysts and their abundances in the associations of the salinity layer of the bottom sediments of the White Sea allowed us to distinguish the following principal types of associations, whose spatial distribution is controlled, first, by the feeding type and composition of dinoflagellates that produce their cysts in the photic layer of the White Sea waters [28, 41].

**The first (autotrophic) association** includes species of the *Gonyaulacaceae* genus (*Operculodinium centrocarpum*, *Spiniferites* spp., and others) and cysts of the *Peridinium* (*Pentapharsodinium dalei*) genus with an autotrophic type of feeding; it almost universally dominates in the recent sediments of the White

Sea (Fig. 4, Table 2). Their maximum total contents in the composition of the associations are determined in the central part of the sea (up to 95%) and in the region of the Solovetskie Islands (70%), where the minimal particulate matter concentrations and, therefore, conditions more favorable for photosynthesis were observed.

The second (heterotrophic) association is mainly represented by cysts of the *Protoperidinium* genus such as *Islandinium minutum* I. *cezare*, *Echinidinium karaense*, *Brigantedinium cariacense*, and *Brigantedinium simplex* (Fig. 4; Table 2). Their maximal contents in the composition of the associations (up to 47%) are rather clearly confined to the inner parts of shallow-water unstratified bays with high water turbidity, first of all, to the near-mouth regions of the Onega and Severnaya Dvina rivers.

## CONCLUSIONS

The studies of the dinocyst distribution in the surface sediments of the White Sea allowed us to reveal the following features of their species composition and quantitative content in the sediments:

(1) The concentrations of dinoflagellate cysts in the sediments of the White Sea are 20 times as low as those calculated previously for the Barents Sea [46] and are compatible with the values obtained for other Arctic seas, for example, for the Laptev Sea [30]. Their quantitative distribution over the White Sea is controlled by the grain-size composition of the sediments, which is responsible for the preservation and conditions of existence of cysts, and by the salinity of the surface waters, which governs the number of planktonic species of dinoflagellates.

(2) The qualitative composition of the dinocyst associations is directly related to the composition of dinoflagellates at the planktonic stage.

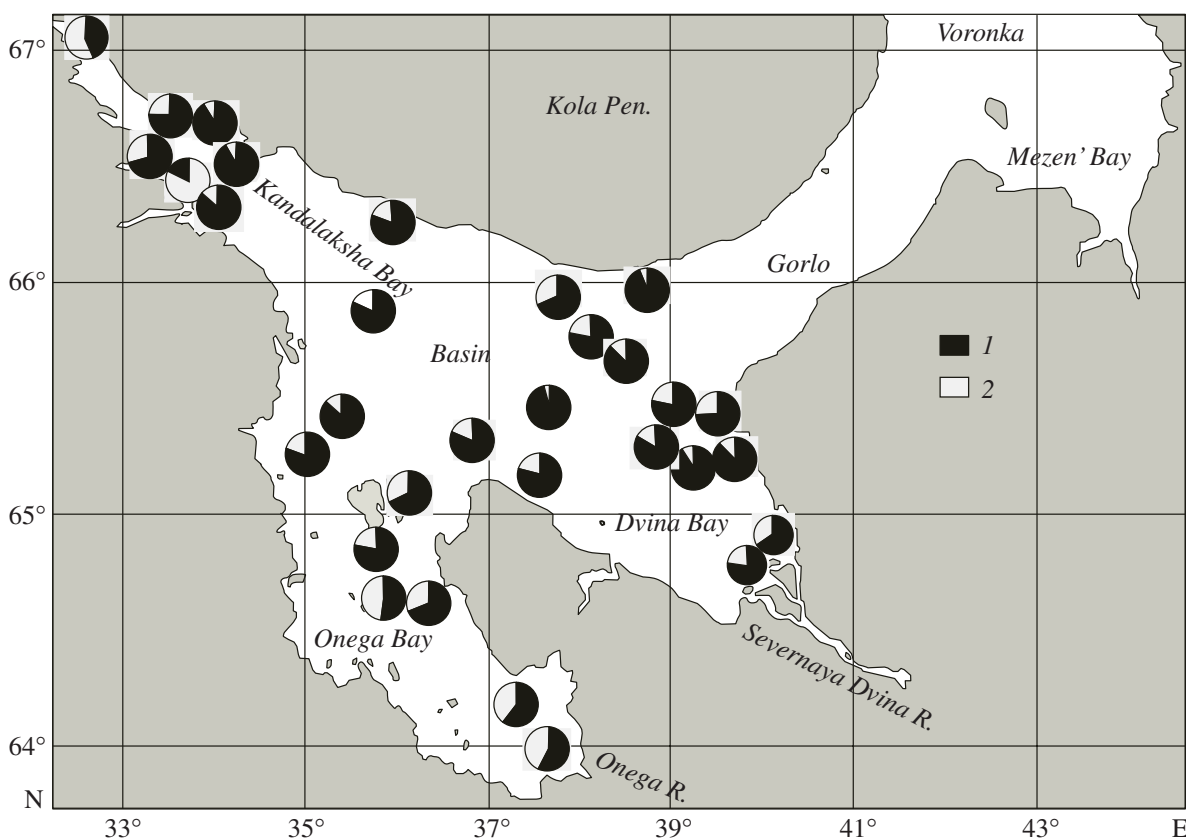
(3) The cysts of autotrophic species, which almost universally dominate in the sediments, reflect the hydrological conditions in the White Sea favorable for their development during the vegetation period.

(4) Studies of the relations between the cysts of autotrophic and heterotrophic dinoflagellate species showed that, in the top parts of shallow-water bays, where active water mixing occurs accompanied by an increase in the water turbidity and the riverine runoff is intensive and rich in microelements and phytoplankton, the proportion of heterotrophic species grows, while, in the open sea areas, representatives of autotrophic species of dinoflagellate cysts absolutely dominate.

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**Fig. 4.** Distribution of the principal types distinguished in the associations of dinoflagellate cysts in the surface sediments of the White Sea, % of the total dinocyst abundance in the samples. The circular diagrams represent the samples in which the statistically required cyst number (no less than 100) were counted. Association 1—autotrophic species of dinoflagellate cysts; association 2—heterotrophic species of dinoflagellate cysts.

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